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The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species

Running headline: Climate warming and colonization potential

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Summary

1. A large number of alien plant species have been introduced as ornamental garden plants to Europe, but relatively few have become invasive. Low climatic suitability may be limiting

the current invasion potential of many alien ornamental species. However, with ongoing disturbance and climate change, this barrier may be reduced for some species.

2. Here we tested how colonization ability (a prerequisite for invasion) of frequently planted alien ornamentals depends on disturbance and heating, and on their species characteristics. We sowed seeds of 37 non-naturalized alien herbaceous garden-plant species into native grassland plots with and without disturbance, and with and without infrared heating lamps. To assess whether their responses differ from those within the regional wild flora, we also sowed 14 native species and 12 naturalized alien species. During two years, we assessed the likelihoods of germination, first-year survival, second-year survival and flowering of these 63 study species.

3. The heating treatment, which also reduced soil moisture, decreased all measures of colonization success, but more so for sown native species than for the non-naturalized and naturalized alien ones. The disturbance treatment increased colonization success, and because heating decreased productivity of the undisturbed grassland plots, it also increased invasibility of these plots. Average colonization success of non-naturalized aliens was reduced by heating, but some species were not affected or performed even better with heating, particularly those with an annual life span and a high seed mass. Winter hardiness improved colonization ability of non-naturalized aliens, but this advantage was reduced in the heated plots.

4. *Synthesis.* Disturbance increased and heating decreased the absolute colonization success of most of the 63 species sown. However, heating had stronger adverse effects on the resident grassland and sown native species than either type of sown alien species. Together, these results suggest that some alien plants may have greater colonization success relative to native plants under a warmer climate.

Key-words: biological invasions, climate change, climate warming, exotic species, functional traits, garden plants, invasion debt, invasion ecology, plant colonization, vegetation disturbance

Introduction

Ornamental horticulture is a major pathway of alien plant introduction (Hulme 2011). In addition, ornamental horticulture often selects and breeds species with traits promoting invasion success, such as easy germination, fast growth and high reproductive output (Weber 2003; Anderson, Galatowitsch & Gomez 2006; Kitajima *et al.* 2006, Trusty *et al.* 2008; Pemberton & Liu 2009; Chrobock *et al.* 2011; Moodley *et al.* 2013). As a result, more than half of Europe's currently naturalized and invasive alien plant species (i.e. those sustaining long-term wild populations, and those spreading across the landscape, respectively; Richardson *et al.* 2000) are escaped ornamental garden plants (Lambdon *et al.* 2008; Essl *et al.* 2011). Therefore, ornamental plants are of particular concern when trying to identify potential future invaders.

As globalization and ornamental plant trade increase, it is probable that many more species will be introduced and become invasive (Essl *et al.* 2011; Seebens *et al.* 2015). Furthermore, as suggested by distribution modelling for Europe (Dullinger *et al.* 2017), climate change is likely to increase the overall naturalization risk of ornamental garden plants that are already widely planted. Identifying those ornamental alien species that are likely to become invasive in the future will thus be an important step towards preventing many future invasions. Once an alien species has passed the introduction barrier, its invasion potential under future climates will depend on its ability to pass subsequent barriers to colonization and establishment (Hellmann *et al.* 2008). Therefore, as a first step, one should assess the effect

of climate change on the ability of introduced non-naturalized alien plants to colonize resident communities.

A species' climatic niche is a key determinant of naturalization success (e.g. Feng *et al.* 2016), and is generally highly conserved from the native to the introduced range (Petitpierre *et al.* 2012; but see Early & Sax 2014). Determining climatic suitability is therefore crucial for assessing a species' potential invasion success. However, the global climate is rapidly changing (IPCC 2014), and many alien species that do not pose an invasion risk under the current climate, may become invasive under future climates (Walther *et al.* 2007, Walther *et al.* 2009). Some of these future invaders may be species recently-introduced to the ornamental garden flora, because they are likely to thrive in emerging warmer climates (Theoharides & Dukes 2007; Bradley *et al.* 2012). However, many future invaders may be alien species that are already widely planted in gardens, but have not yet naturalized due to an unsuitable climate (van der Veken *et* al. 2008; Feng *et al.* 2016; Dullinger *et al.* 2017). Gardens and nurseries may thus provide convenient jumping-off points for invasion under climate change (van der Veken *et al.* 2008).

Invasion success is frequently facilitated by disturbance of resident communities, as the introduced alien species take advantage of the reduced competition and changes in resource availability (Hobbs 1989). Indeed, more disturbed grasslands have been generally found to be more easily invaded than less disturbed ones (e.g. Burke & Grime 1996; Gross, Mittelbach & Reynolds 2005; Kempel *et al.* 2013). Some introduced aliens, however, may have a higher ability to colonize undisturbed grasslands than others. Species traits are likely to affect this potential, and may differentially contribute to a species' colonization ability in disturbed and undisturbed grassland sites under ambient and future climatic conditions.

To test whether invasion risk of ornamental non-naturalized alien plants is likely to increase with climate change and disturbance, we conducted an introduction experiment in a

grassland site in Germany. We sowed 37 non-naturalized alien species commonly grown as ornamentals in European gardens, as well as 12 naturalized alien and 14 native species. We aimed to obtain more generalized results by using a large number of species (van Kleunen *et al.* 2010, van Kleunen *et al.* 2014). Specifically, we addressed the following questions:

(1) How does colonization success of currently non-naturalized alien herbaceous species respond to increased temperatures and disturbance, and how do these responses differ from those of natives and naturalized aliens?

(2) How do traits of non-naturalized alien species affect colonization success in the different temperature and disturbance treatments?

Methods

STUDY SPECIES

Non-naturalized alien species for this introduction experiment were chosen from the European Garden Flora (EGF), a comprehensive encyclopaedia of plant species grown in many European gardens (Cullen *et al.* 2011; see Table S1 in Supporting Information). We selected 37 ornamental herbaceous species, covering 18 families, based on the criteria that they are alien to Germany and not naturalized there. Furthermore, to ensure that these species spanned a climatic suitability gradient, we selected species from each of the five outdoor hardiness zones used by the EGF (Table S1). These hardiness zones are defined based on the minimum temperatures at which a species can survive. We designated these zones as 1-5, with the least hardy (hardiness zone 1) species only tolerating winter minimum temperatures above -5°C and the hardiest (hardiness zone 5) species surviving winter minimum temperatures below -20°C (Table S1). We classified species as having either an annual or perennial life span based on information in the EGF, and we compiled data on their average

seed mass (range: 0.09-19.52 mg) from B & T World Seeds (Aigues-Vives, France) or our own measurements.

We also compared colonization success of the 37 non-naturalized alien species with that of 14 native (from 13 families) and 12 naturalized alien species (from nine families) that occur in the wild in Germany. We included fewer of the latter two types of species, because our primary interest was the colonization success of the non-naturalized aliens. Although this may have introduced minor sampling effects, this is unlikely to have substantially affected the results, because the total number of species used was large. The native and naturalized alien species were chosen based on the criteria that they are known to occur in grasslands but are not part of the resident grassland community in our experimental garden site (see below). To increase the generalizability of the results, species from all three groups (native, naturalized alien and non-naturalized alien) were selected to cover a broad range of families, and included both annual and perennial species. Seeds of the non-naturalized and naturalized alien species were obtained from B & T World Seeds, and seeds of the native species were obtained from Rieger-Hoffman GmbH (Blaufelden-Raboldshausen, Germany). To be able to account for variation in the quality of the seeds, we assessed germination rates under optimal conditions in a separate greenhouse experiment (see Figure S1).

STUDY SITE AND EXPERIMENT

We conducted this study in a grassland site (further referred to as 'resident grassland') in the Botanical Garden of the University of Konstanz, Germany (47.69° N, 9.18°E). The 2000-2010 average mean annual temperature in Konstanz is 9.8°C, and average mean annual precipitation is 1048.4 mm (World Weather Online 2016). Konstanz lies within the EGF hardiness zone 3 (i.e. winter minimum temperatures from -10 to -15°C). The resident grassland for our experiment was established from a commercial seed mixture for

mesotrophic grasslands (02 Fettwiese, Rieger-Hoffman, Blaufelden-Raboldshausen, Germany), including seeds of 39 common German grassland species (11 grasses, 28 forbs; Table S2). To ensure that the resident grassland was well-established at the start of our introduction experiment, the seed mixture was sown one year in advance (April 2013).

The climate-warming treatment in this study was applied using infrared-heating lamps (MRM-2420, 240V, 2000W, Kalglo Electronics Co., Bethlehem, USA). The infrared-heating lamps were 1.65 m long and 12 cm wide, and positioned at a height of 1.45 m above the soil surface using metal frames. Each lamp was positioned above a 2 m × 2 m plot of the resident grassland, and with the help of a small motor slowly swayed like a pendulum along its horizontal axis to evenly heat the entire plot (Fig. S2). We had ten replicate resident grassland plots with infrared-heating lamps, and each of these plots was paired with an adjacent unheated plot that also had metal frames but no lamps. To avoid interference among plots, we had a 0.8 m wide buffer between adjacent plots.

The temperature of each of the 20 plots was measured once every two seconds with infrared temperature sensors placed 75 cm above the ground, at an angle of ~45°. The average difference in canopy temperature between heated and control plots across the two years of the experiment was 1.6°C (SE=0.04°C) (Fig. S3). This experimental temperature increase is within the 1.5-3.5 °C range of predicted air temperature increases for Konstanz and much of Europe by the end of the 21st century under mitigating climate scenarios (Füssel & Pol 2012). Experimental heating is likely to reduce soil-water availability, another component of climate change, by increasing the water-vapour gradient and conductance (Kimball 2005; de Boeck *et al.* 2010). Therefore, we also measured the soil-moisture levels in each plot three times during the study using a HH2 moisture meter attached to a WET-2 WET sensor (Delta-T Devices Ltd, Cambridge UK; Fig. S4).

To speed up growth of the resident grassland prior to the start of the experiment (i.e. sowing of the target species), we fertilized it in August 2013 with Universol Blue® (Everris; Nordhorn, Germany, 10 g per m^2) with an effective rate of ~1.8 g N (1 g nitrate, 0.8 g ammonium) applied per m^2. All plots were mown in September 2013, and again in April 2014. As a disturbance treatment, five randomly chosen heated/unheated plot pairs were hand-tilled to a depth of ~15 cm in April 2014. Each plot was then divided into 64 subplots of 20 cm × 20 cm marked with orange-painted bamboo sticks (Fig. S2).

Each of the 37 non-naturalized alien, 12 naturalized alien and 14 native target species was randomly allocated to one subplot per plot. This resulted in five independent replicate subplots per species in each of the four heating-by-disturbance treatment combinations. On 23 April 2014, 50 seeds of each species were sown in their respective subplots. Some previous introduction studies sowed fewer seeds of species with heavy seeds than of species with lighter seeds to manipulate total mass, rather than total number, of seeds added (e.g. Burke & Grime 1996). However, because colonization success is likely to increase with propagule pressure (Lockwood *et al.* 2005), we sowed a fixed number of seeds per species. We did not do any supplemental watering (i.e. the plants relied on natural precipitation).

Six weeks after sowing (from 2 – 5 June 2014), we checked seed germination success of each species in a plot. As there was no buffer between subplots in a plot, we also looked for seedlings of the species in neighbouring subplots to check whether seeds had inadvertently moved outside their allocated subplots. After that first census, we counted the number of seedlings and plants of the sown species at the beginning of each month until October 2014 (i.e. we had a total of five censuses in the first year). As most grasslands in Central Europe are mown at least once a year (Blüthgen *et al.* 2012), all plots were mown in November 2014. The mown plant material was left on the plots. We again counted the number of seedlings and plants of the sown species in 2015, beginning on 30 March, and

subsequently once a month until October (i.e. we had a total of seven censuses in the second year). At each of the 12 censuses, we also scored the presence of any flowering individuals of the target species as a binary measure of flowering success per subplot.

To test effects of disturbance and heating on the resident grassland, we assessed resident grassland diversity, composition and productivity. To assess diversity and composition, we estimated the percentage cover of all species present for each plot in August 2014. To estimate plot productivity, we harvested total above-ground biomass of the resident grassland in three randomly selected subplots without any target species in November 2014. This was done immediately before mowing the entire plots, and it was repeated in November 2015. The biomass samples were dried at 70°C for >72 h and then weighed.

STATISTICAL ANALYSES

Effects of heating, disturbance and species status on colonization success

We used generalized linear mixed effect models (GLMMs) to test whether heating (yes, no), disturbance (yes, no), species status (non-naturalized alien, naturalized alien, native) and their interactions significantly affected colonization success of the experimentally introduced species. We used four measures of colonization success as response variables: 1) germination likelihood: a binary measure (yes, no) of whether any seedlings of the sown species were present in any census, 2) first-year survival: the proportion of the 50 originally sown seeds that had germinated and subsequently survived until the end of the first year's growing season (i.e. until the October 2014 census), 3) second-year survival: the proportion of the 50 originally sown seeds that had germinated and subsequently survived until the end of the second year's growing season (i.e. until the October 2015 census), and 4) flowering likelihood: a binary measure (yes, no) of whether any individual of the target species in a subplot flowered at any point during the experiment. The GLMMs were built using binomial

error distributions using a logit link, with the *glmer* function of the *lme4* package (Bates *et al.* 2015) in R 3.3.0 (R Core Team 2016). To account for non-independence of subplots within a plot and plots within a pair, plot and plot pair were included as nested random effects. To account for non-independence of replicates of a species and for phylogenetic non-independence of species, we included species and family as nested random effects. To account for variation in the viability of the seeds, we included a covariate in all models, which was the germination rate for each species as measured under optimal conditions in a separate greenhouse experiment (Fig. S1). We assessed the significance of each fixed term with a likelihood-ratio test of the change in deviance between a model with and a model without the term of interest (Zuur *et al.* 2009). Resident grassland composition, diversity and biomass were not included in these models, because of limited statistical power. Therefore, these grassland variables were instead analysed separately (see below).

Effects of traits on colonization success of non-naturalized aliens

To test whether colonization success of the 37 non-naturalized alien species was related to their traits, we modelled our four measures of colonization success (germination likelihood, first-year survival, second-year survival, flowering likelihood) as functions of species hardiness zone (1-5), life span (annual, perennial), average seed mass (standardized to a mean of zero and a standard deviation of one) and their interactions with disturbance (yes, no) and heating (yes, no). To facilitate interpretation of the results, hardiness zone was included as a continuous variable and also standardized to a mean of zero and a standard deviation of one.

The models included main effects of each species trait as well as their two- and three-way interactions with heating and disturbance. Interactions between species traits were not considered. We included plot nested within plot pair and species nested within family as random effects, and germination rate under optimal conditions in the greenhouse as a

covariate. Because the species-trait models included non-experimental variables (i.e. traits) and many interactions, we used Akaike Information Criterion (AIC)-based model selection (Akaike 1973) to select the most parsimonious models. For each response variable, all fixed terms were individually removed from the saturated model in order of least significance, and terms whose removal did not result in an AIC increase > 4 were excluded. This stepwise removal of fixed terms was repeated until we had a minimum adequate model.

Effects of treatments on resident grassland

To test effects of heating and disturbance on the species composition of the resident grassland plots, we first created a Bray-Curtis dissimilarity matrix from the species-cover data using the vegdist function of the *vegan* package (Oksanen *et al.* 2016). Then we used the *adonis* function to perform a PERMANOVA with heating, disturbance and their interactions as fixed terms and plot pair as a random effect. We additionally used the species-cover data to calculate the Shannon Diversity Index using the *diversity* function of the *vegan* package (Oksanen *et al.* 2016). To test whether the Shannon Diversity Index was significantly affected by disturbance, heating and their interaction, we then performed an ANOVA using the *lmerTest* package (Kuznetsova, Brockhoff & Christensen 2015) with plot pair included as a random effect.

To test whether productivity of the resident grassland was significantly affected by disturbance, heating and their interaction, we performed an ANOVA with aboveground biomass of the subplot as the response variable. Disturbance and heating treatments, the year of harvest (2014, 2015), and all two-way interactions of the three factors were included as fixed terms. To account for non-independence of plots within a pair, and subplots within a plot, plot pair and individual plot were included as nested random effects.

Results

Among the sown species, 33 out of 37 (89.2%) non-naturalized alien, 11 out of 12 (91.7%) naturalized alien and 12 out of 14 (85.7%) native species had at least one seed that germinated (Fig. S5). Twenty (54.1%) non-naturalized alien, five (41.7%) naturalized alien and seven (50.0%) native species had at least one plant that survived the first year (Fig. S6). Eight (21.6%) non-naturalized alien, four (33.3%) naturalized alien and five (35.7%) native species had at least one plant that also survived to the end of the second growing season (Fig. S7). Fourteen (37.8%) non-naturalized alien, five (41.7%) naturalized alien and five (35.7%) native species had at least one plant that flowered during the two years of the experiment (Fig. S8).

EFFECTS OF HEATING AND DISTURBANCE ON NON-NATURALIZED ALIEN, NATURALIZED ALIEN AND NATIVE SPECIES

The likelihoods of germination, first-year survival, second-year survival and flowering were all lower in undisturbed than in disturbed plots, and this was statistically significant for all colonization-success metrics except flowering likelihood (Tables 1, Figs 1, 2). Heating had a negative effect on colonization success on average, as shown by reductions in germination, first-year survival, second-year survival and flowering of species in heated relative to unheated plots (Table 1). The negative effects of heating on germination and first-year survival were stronger in disturbed than in undisturbed plots (significant heating x disturbance interactions in Table 1; Fig. 2), which was presumably the result of very low colonization success in undisturbed plots.

Non-naturalized alien, naturalized alien and native species did not, on average, perform significantly differently from one another (Table 1). However, heating had a stronger

negative effect on native species than on naturalized and non-naturalized alien species for our four colonization-success metrics (Table 1, Fig. 2). On the other hand, in undisturbed plots, native species were more likely to germinate than non-naturalized and naturalized alien species, and had higher first-year survival and second-year survival than non-naturalized alien species (Table 1, Fig. 2).

EFFECTS OF TRAITS ON COLONIZATION SUCCESS OF NON-NATURALIZED ALIEN SPECIES

Colonization success of the non-naturalized alien species was low in undisturbed plots and was negatively affected by heating (Fig. 2). Nevertheless, several of the non-naturalized alien species performed as least as well in the heated plots as in the unheated plots. For first-year survival, these species included *Centaurea americana*, *Centaurea macrocephala*, *Eritrichium canum*, *Iris domestica* and *Zinnia peruviana* (Fig. 1).

Averaged across all treatments, annual and perennial non-naturalized alien species did not differ in their colonization success. However, in disturbed plots, annuals were more likely to germinate than perennials, whereas in undisturbed plots, the reverse was true (Table 2, Fig. 3a). In unheated plots, first-year survival of perennials was higher than that of annuals, but in heated plots annual first-year survival was slightly higher than that of perennials (Table 2, Fig. 3b).

Germination and first-year survival of non-naturalized alien species increased significantly with seed mass, and there was a similar but non-significant trend for second-year survival (Table 2, Fig. 3c, d, e, f). The positive effect of seed mass on germination was only apparent in the disturbed plots (Fig. 3d), whereas the positive effect on first- and second-year survival was weaker in the disturbed than in the undisturbed plots (Table 2, Fig. 3e, f).

Moreover, the positive effect of seed mass on first-year survival was stronger in heated than in unheated plots (Table 2, Fig. 3c).

Averaged across all treatments, winter hardiness of the non-naturalized alien species did not affect the four colonization-success metrics (Table 2). However, it had a positive effect on first-year survival in the disturbed plots; this positive effect was smaller in the undisturbed plots (Table 2, Fig. 3g). Although winter hardiness had a positive effect on second-year survival in unheated plots, this effect was reduced in heated plots (Table 2, Fig. 3h).

EFFECTS OF HEATING AND DISTURBANCE ON THE RESIDENT GRASSLAND

The resident grassland contained 60 native and four alien plant species (Table S2). The Shannon Diversity Index of the plots was not significantly affected by the main effects of disturbance ($F_{1, 8}$=0.01, p=0.910) and heating ($F_{1, 8}$=2.41, p=0.159). However, there was a significant interaction between heating and disturbance; diversity decreased with heating in disturbed plots, but increased slightly with heating in undisturbed plots ($F_{1, 8}$=5.73, p=0.044; Fig. S9). In the analysis of species composition, NMDS-axis 1 clearly separated the disturbed and undisturbed plots. NMDS-axis 2 separated the heated and unheated plots, but to different degrees for disturbed and undisturbed plots (Fig. S10). In the PERMANOVA, these differences in species composition were reflected in significant effects of disturbance ($F_{1, 8}$=19.41, p=0.004), heating ($F_{1, 8}$=1.16, p=0.018) and their interaction ($F_{1, 8}$=1.48, p=0.002).

Biomass production was significantly higher in undisturbed than in disturbed plots ($F_{1, 114}$=10.45, p=0.001; Fig. S11), but this disturbance effect was only apparent in the first year as indicated by the significant year x disturbance interaction ($F_{1, 114}$=6.92, p=0.01). The effect of heating also differed significantly between the two years ($F_{1, 114}$=4.26, p=0.04). In

the first year, heating had a slight positive effect on biomass production, whereas in the second year it had a negative effect (Fig. S11).

Discussion

In our species-introduction experiment, disturbance of resident grassland strongly promoted colonization success of the sown species. Heating had a negative effect on colonization success, but more so for native than for non-naturalized and naturalized alien species. Nevertheless, some species did not exhibit reduced colonization success in response to heating, and a few even responded positively to the simulated future temperatures (Figs 1 and 2). Among non-naturalized alien species, neutral or positive responses were associated with an annual life cycle and heavy seeds, while the advantage of high winter hardiness was reduced under warmer temperatures.

COLONIZATION SUCCESS OF NON-NATURALIZED ALIEN, NATIVE AND NATURALIZED ALIEN SPECIES

Our findings suggest that most of the species we included in our experiment are not well-suited to an increase in temperatures at our study location. This contrasts with the positive responses of introduced species to increased temperatures observed elsewhere (e.g. Verlinden & Nijs 2010; Chuine *et al.* 2012; He, Li & Peng 2012; Liu et al. 2016). Our results suggest that colonization success of incoming species will be determined by their ability to tolerate warmer climates. Consistent with other grassland introduction experiments (e.g. Kempel *et al.* 2013), we found that undisturbed grassland plots were highly resistant to colonization. Only six of the 63 species that we sowed into the plots showed any first-year survival in undisturbed plots (four native species: *Achillea millefolium*, *Ajuga reptans*, *Aquilegia vulgaris* and *Vicia sepium*, and two non-naturalized alien species: *Iris domestica* and

Monarda punctata). However, first-year survival of sown plants was slightly higher in heated than in unheated undisturbed plots. Heating may have a direct effect on the performance of the sown species, but might also indirectly affect colonization by altering the composition of the resident community. Heating reduced diversity in the plots with a disturbed resident grassland community, and it reduced biomass production of both disturbed and undisturbed plots in the second year.

It is difficult to separate the direct effects of heating on colonization from the indirect effects of heating on the resistance offered by the resident plant community, and we did not have sufficient statistical power to test these effects directly. However, if the resident grassland community was negatively impacted by heating, it is likely that the sown species benefited from reduced competition with the resident community, resulting in greater rates of colonization. In the second year of our experiment, biomass production of the resident grassland was significantly lower in heated than in unheated plots (Fig. S11). This reduction in resident biomass could decrease cover and increase availability of open niches for establishment (Burke & Grime 1996; Davis, Grime & Thompson 2000; Gross, Mittelbach & Reynolds 2005; Thuiller *et al.* 2005; Ward & Masters 2007; Thuiller *et al.* 2011; Chuine *et al.* 2012). Thus, higher future temperatures might lower the barrier to invasions by more resistant aliens into physically undisturbed, but less productive communities.

Consistent with projected climate change in Central Europe, our climate-warming treatment also resulted in reduced soil moisture in the heated plots (Fig. S4). Unusually high ambient summer temperatures during our 2014-2015 study period (Climate Data Online 2016) may have further reduced soil moisture levels beyond the effects expected from the infrared lamps alone. Indeed, it is likely that reduced soil moisture at least partly produced the observed responses to heating. De Boeck *et al.* (2011) showed that heat waves had little negative impact on plant growth unless they were combined with drought.

The native species that we sowed were better colonizers of the undisturbed resident grassland than either non-naturalized or naturalized alien species. This suggests that the natives are more suited to competing and establishing in these grassland communities than the alien species. However, the negative impact of heating on colonization was stronger for native species than for either group of alien species. This suggests that native species may be less pre-adapted to establish new populations under climate change than aliens. As described above, the heated undisturbed resident grassland plots were also slightly less resistant to sown species and were less productive than unheated plots. Together these results suggest that native species in general will be less tolerant than alien species of the effects of warming under climate change, resulting in a relative advantage for alien species.

Naturalized and non-naturalized alien species were more similar to one another in colonisation success than either group was to the sown native species. Naturalized species are presumably already suited to current climates in Central Europe (Feng *et al.* 2016). However, they may also frequently occupy broader temperature niches in their introduced ranges (Leiblein-Wild, Kaviani & Tackenberg 2014). This broad environmental tolerance might explain why naturalized alien species in our experiment were better colonizers under heating than the native species that we sowed. The similarity in the performance of the naturalized and non-naturalized aliens suggests that the non-naturalized aliens may also have a broad environmental tolerance. Selective introduction or breeding of non-naturalized alien species with more plastic genotypes may also predispose them to be more tolerant of climate change (Bossdorf, Lipowsky & Prati 2008). Ultimately, this means that many of the widely-cultivated alien species in Central Europe possess the potential to become naturalized (and in some cases invasive) in the future (Dullinger *et al.* 2017).

Despite the large scale of our experiment, the 37 non-naturalized alien species that we used still only represent a small fraction of Europe's potential future invaders. Yet we identified several currently non-naturalized alien species that are likely to colonize under future climatic conditions. Moreover, we identified traits associated with colonization success, which could be used to identify other non-naturalized alien species that are more likely to colonize in the future.

Perennial non-naturalized alien species were more likely to germinate than annual ones in undisturbed grassland plots. Annual species are known to be poor competitors in stable environments with established vegetation, due to limited long-term investment in resource-acquisition and storage organs (Pitelka 1977). In response to heating, however, annual species first-year survival increased, and perennial first-year survival decreased. We did not test priority effects in this study, but it is possible that the fast initial root growth often associated with annuals (Struik 1965; Harris & Wilson 1970; Roumet, Urcelay & Diaz 2006) may allow them to quickly access limited resources such as water. Thus, under changing climates and increasing disturbance, annual species may be better able to colonize and ultimately naturalize.

Our findings that seed mass increased colonization success mirrored those of Jakobsson & Eriksson (2000) and Kempel *et al.* (2013), showing greater survival for species with heavier seeds in undisturbed plots. The higher initial resource availability in heavier seeds might confer a growth advantage that increases subsequent seedling survival when competing with intact vegetation (Moles & Westoby 2004). Survival for species with heavier seeds was also greater in heated than unheated plots. This may be because species with heavier seeds germinate and survive as seedlings better in moisture-limited environments than those with smaller seeds (Khurana & Singh 2000). Under climate change, non-

naturalized alien species with heavier seeds may therefore have a colonization advantage, and thus may be more likely to naturalize if they can disperse to suitable sites. However, it should be noted that species with lighter seeds may also produce more of them per plant, and be more widely dispersed than heavier seeds (Jakobsson & Eriksson 2000). Thus, greater propagule pressure of lighter-seeded colonizing species might compensate for poorer individual survival. As we did not assess seed production and dispersal ability of our species, our experiment was unable to test this.

The effect of winter hardiness of non-naturalized alien species on their colonization success depended on disturbance and heating. While first-year survival was not strongly affected by hardiness in disturbed plots, it increased with hardiness in undisturbed plots. The lower climatic suitability of the less hardy species may have been exacerbated by competition in the undisturbed plots. Although winter hardiness is likely to be associated with various aspects of climatic tolerance, including drought tolerance (Thomashow 1999; Zhu 2002; Pembleton & Sathish 2014), it is primarily a measure of the winter temperature that a species can tolerate. Our study site lies in hardiness zone 3 (minimum temperatures reaching roughly -10 to -15°C), and therefore we would expect species from the less hardy zones 2 and 1 (minimum temperatures down to -10 and -5°C, respectively) to benefit from heating. Indeed, we found that for survival until the end of the second growing season, which included overwinter survival, the advantage of hardier species over less hardy species was reduced in the heated plots. While less-hardy species may not exhibit an absolute increase in suitability under changing climates, if hardier species' climatic suitability is reduced, opportunities for the colonization of less-hardy species may nevertheless increase.

Conclusions

We simulated and measured the effects of climate-warming on the colonization of a semi-natural grassland by 37 non-naturalized species, under realistic field conditions. We identified five species that were able to successfully colonize and may be able to naturalize under warming climates (*Centaurea americana*, *Centaurea macrocephala*, *Eritirichium canum*, *Iris domestica* and *Zinnia peruviana*). Three of these species have already become naturalized elsewhere in the world (*C. americana*, *I. domestica* and *Z. peruviana* are naturalized in at least 11, 79 and 39 regions outside Europe, respectively; van Kleunen *et al.* 2015). We also identified higher seed mass and an annual life span as traits that may make a species more tolerant to warming climates, while the advantage of greater winter hardiness may be reduced under climate change. These traits may be useful in identifying further potential invaders. Overall, increased temperatures negatively impacted non-naturalized alien colonization. However, native species were more strongly affected. Therefore, even if the majority of ornamental alien species will be climatically less suited to Europe in the future, some of the ornamental alien species may benefit from the niches left vacant by the more strongly affected native species.

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.c4t44 (Haeuser, Dawson & van Kleunen 2017).

Statement of authorship

MVK and WD designed the study. EH implemented the study, collected the data, did the analyses with inputs from MVK and WD, and wrote the first draft of the manuscript.

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Supporting information

Table S1: Native, naturalized and non-naturalized species selected for introduction as seeds in the experimental grassland with and without disturbance and with and without heating.

Table S2: Species found in the resident grassland.

Figure S1: Means and standard deviations of optimal germination rate for all target species.

Figure S2: One of the experimental plots heated by an IR-heater lamp (and disturbed by soil tilling prior to sowing the study species).

Figure S3: Daily average difference in temperature between heated and unheated treatments, across plots, during the entire experiment.

Figure S4: Soil-moisture percentage (mean and standard error) in disturbed vs. undisturbed, and unheated vs. heated plots.

Figure S5: Germination likelihood and its standard error of the non-naturalized alien (top), native (center) and naturalized (bottom) introduced species in heated and unheated and disturbed and undisturbed plots.

Figure S6: Proportion and standard error of sown seeds that germinated and were surviving at the end of the first year, according to identity of the introduced native (top) and naturalized (bottom) species, disturbance and heating treatments.

Figure S7: Proportion and standard error of sown seeds that germinated and were surviving at the end of the second year, according to identity of the non-naturalized alien (top), native (middle) and nautralized (bottom) introduced species, in the disturbance and heating treatments.

Figure S8: Flowering likelihood and standard error of the non-naturalized alien (top), native (center) and naturalized (bottom) introduced species in heated and unheated plots. Results are shown only for disturbed plots, as no flowering occurred in undisturbed plots.

Figure S9: Shannon Diversity Index (means and standard errors) of the resident community in grassland plots of the different combinations of the disturbance and heating treatments.

Figure S10: Ordination plot of resident grassland species composition based on a Bray-Curtis dissimilarity matrix.

Figure S11: Aboveground biomass per subplot (means and standard errors) in November 2014 and November 2015 in each combination of the disturbance and heating treatments.

Table 1. Results of generalized linear mixed effects models testing the significance of effects of species status (introduced native, naturalized or non-naturalized), heating and disturbance on different measures of colonization success. Optimal germination rate refers to the germination under greenhouse conditions. Significance of the fixed terms was tested using log-likelihood ratio tests comparing models with and without the term of interest. Order indicates the sequence in which fixed terms were removed from the model. Marginal and conditional R^2 values (calculated using the *sem.model.fits* function in the *piecewiseSEM* package; Lefcheck 2015) are reported for all saturated models. Bold p values indicate significance ($p<0.05$), and italics indicate marginally significant values ($p<0.1$).

			Germination likelihood		**1st year survival**		**2nd year survival**		**Flowering likelihood**	
Fixed terms	**Order**	**d.f.**	**χ^2**	**P**	**χ^2**	**P**	**χ^2**	**P**	**χ^2**	**P**
Optimal germination rate	4	1	18.14	**<0.001**	26.11	**<0.001**	2.14	0.143	11.3	**<0.001**
Heating	3	1	2.37	0.123	2.85	*0.091*	3.51	*0.061*	5.12	**0.024**
Disturbance	3	1	5.79	**0.016**	20.05	**<0.001**	6.69	**0.010**	37.75	**<0.001**
Species status	3	2	1.81	0.405	0.3	0.859	1.835	0.400	0.3	0.865
Heating : Disturbance	2	1	5.58	**0.018**	10.93	**<0.001**	0.02	0.875	0	1
Heating : Status	2	2	136.56	**<0.001**	728.57	**<0.001**	178.79	**<0.001**	34.35	**<0.001**
Disturbance : Status	2	2	287.03	**<0.001**	5747.4	**<0.001**	560.69	**<0.001**	0.01	0.994
Heating : Disturbance : Status	1	2	74.89	**<0.001**	160.36	**<0.001**	0.23	0.890	0	1
Random terms			**Variance**	**Levels**	**Variance**	**Levels**	**Variance**	**Levels**	**Variance**	**Levels**
Species/Family			5.39	63	28.69	63	21.14	63	56.80	63
Family			0.15	24	<0.01	24	31.81	24	<0.01	24
Plot			0.28	20	0.18	20	1.25	20	0.20	20
Plot pair			1.75	10	0.06	10	2.47	10	0.26	10
R^2			**Marginal**	**Conditional**	**Marginal**	**Conditional**	**Marginal**	**Conditional**	**Marginal**	**Conditional**
			0.27	0.78	0.60	0.96	0.55	0.98	0.77	0.99

Table 2. Results of binomial GLMMs testing significance of the effects of traits (life span, seed mass, winter hardiness) and treatments (disturbance, heating) on different measures of colonization success of ornamental species. Interactions and parameters not found to be significant in the full models were excluded from the final minimum adequate models (indicated as --). Three-way interactions between disturbance, heating and individual traits were tested in all initial full models, but as they were not significant, they were excluded. Random effects of species, family, plot and plot pair were included in all models. Marginal and conditional R^2 values (calculated using the *sem.model.fits* function in the *piecewiseSEM* package; Lefcheck 2015) are reported for all reduced models. Bold p values indicate significance ($p<0.05$), and italics indicate marginally significant values ($p<0.1$).

Traits	**Germination likelihood**				**1st year survival**				**2nd year survival**				**Flowering likelihood**			
Fixed terms	**Est.**	**SE**	**z**	**P**	**Est.**	**SE**	**z**	**P**	**Est.**	**SE**	**z**	**P**	**Est.**	**SE**	**z**	**P**
(Intercept)	-0.52	1.01	-0.52	0.604	**-10.34**	**2.22**	**-4.65**	**<0.001**	**-18.14**	**3.53**	**-5.14**	**<0.001**	**-4.53**	**0.95**	**-4.79**	**<0.001**
Optimal germination rate	**1.36**	**0.32**	**4.31**	**<0.001**	**3.61**	**0.92**	**3.94**	**<0.001**	*8.77*	*4.47*	*1.96*	*0.057*	**1.72**	**0.75**	**2.29**	**0.022**
Heating-Heated	--	--	--	--	0.19	0.94	0.20	0.843	**-1.23**	**0.55**	**-2.23**	**0.026**	--	--	--	--
Disturbance-Undisturbed	**-4.70**	**1.32**	**-3.57**	**<0.001**	**-9.17**	**1.03**	**-8.88**	**<0.001**	**-151.75**	**26.25**	**-5.78**	**<0.001**	-22.57	273.68	-0.08	0.934
Hardiness zone	--	--	--	--	0.65	0.87	0.76	0.449	**4.19**	**2.12**	**1.97**	*0.052*	--	--	--	--
Life span-Perennial	-0.24	0.71	-0.33	0.742	1.65	2.03	0.81	0.420	--	--	--	--	--	--	--	--
Seed mass	**1.79**	**0.42**	**4.21**	**<0.001**	**2.12**	**0.83**	**2.53**	**0.011**	*2.86*	*1.68*	*1.70*	*0.090*	--	--	--	--
Heated : Undisturbed	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Heated : Hardiness	--	--	--	--	--	--	--	--	**-0.67**	**0.05**	**-13.99**	**<0.001**	--	--	--	--
Heated : Perennial	--	--	--	--	**-0.52**	**0.04**	**-12.57**	**<0.001**	--	--	--	--	--	--	--	--
Heated : Seed mass	--	--	--	--	**0.38**	**0.01**	**31.06**	**<0.001**	--	--	--	--	--	--	--	--
Undisturbed : Hardiness	--	--	--	--	**2.52**	**0.30**	**8.53**	**<0.001**	--	--	--	--	--	--	--	--
Undisturbed : Perennial	**2.01**	**0.76**	**2.64**	**0.008**	--	--	--	--	--	--	--	--	--	--	--	--
Undisturbed : Seed mass	**-1.13**	**0.41**	**-2.78**	**0.005**	**1.34**	**0.07**	**19.00**	**<0.001**	**40.12**	**7.12**	**5.64**	**<0.001**	--	--	--	--

Random terms	**Variance**	**Levels**	**Variance**	**Levels**	**Variance**	**Levels**	**Variance**	**Levels**
Species/Family	1.19	37	16.99	37	57.85	37	8.81	37
Family	1.41	18	0.37	18	<0.01	18	<0.01	18
Plot	0.48	20	4.04	20	1.06	20	0.04	20
Plot pair	2.57	10	<0.01	10	6.55	10	0.01	10
R^2	**Marginal**	**Conditional**	**Marginal**	**Conditional**	**Marginal**	**Conditional**	**Marginal**	**Conditional**
	0.40	0.78	0.66	0.96	0.99	>0.99	0.91	0.98

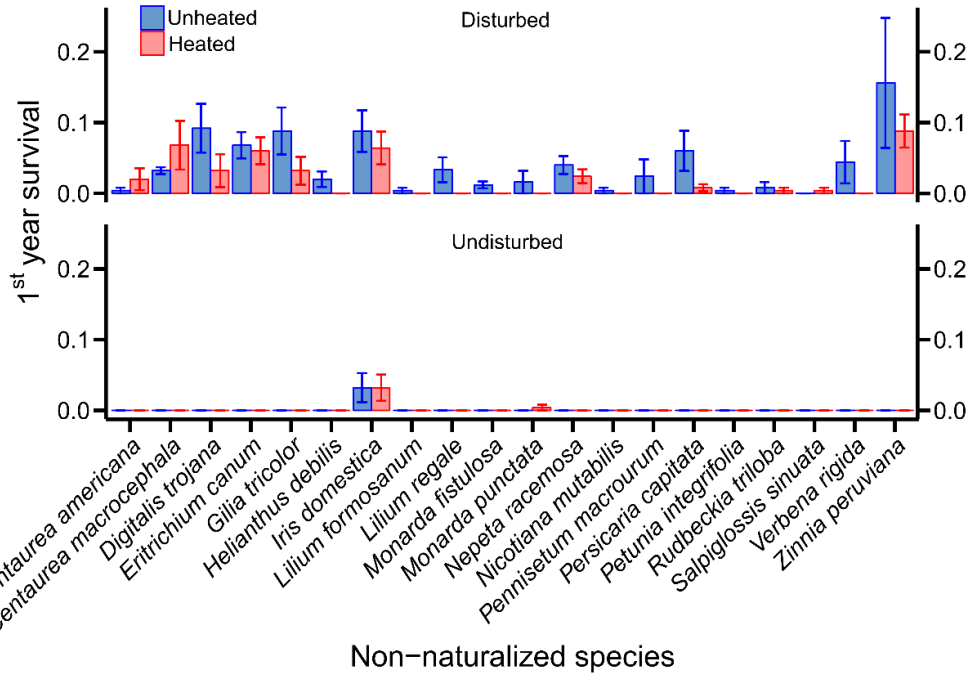

Fig. 1. Proportion of sown seeds of non-naturalized ornamental species that germinated and survived as plants until the end of the first year in the disturbance and heating treatments. Only the 20 species (out of 37) of which at least one seedling survived are shown.

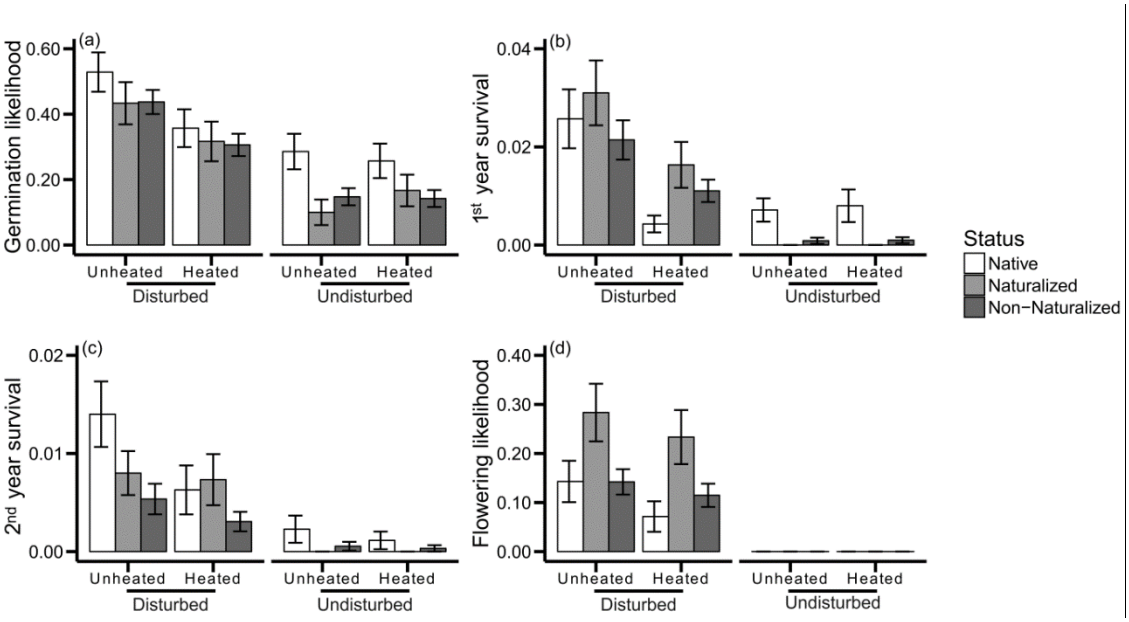

Fig. 2. Colonization success (means and standard errors) for native (white), naturalized (light grey) and non-naturalized (dark grey) introduced species in the heating and disturbance treatments according to the four measured metrics: (a) germination likelihood, (b) first-year survival, (c) second-year survival and (d) flowering likelihood. First-year survival and second-year survival are measured as proportions of the sown seeds in a subplot that are present as seedlings by the end of the first and second growing seasons, respectively. Germination likelihood and flowering likelihood are a measure of the presence (yes, no) of seedlings and flowering plants, respectively, in a subplot.

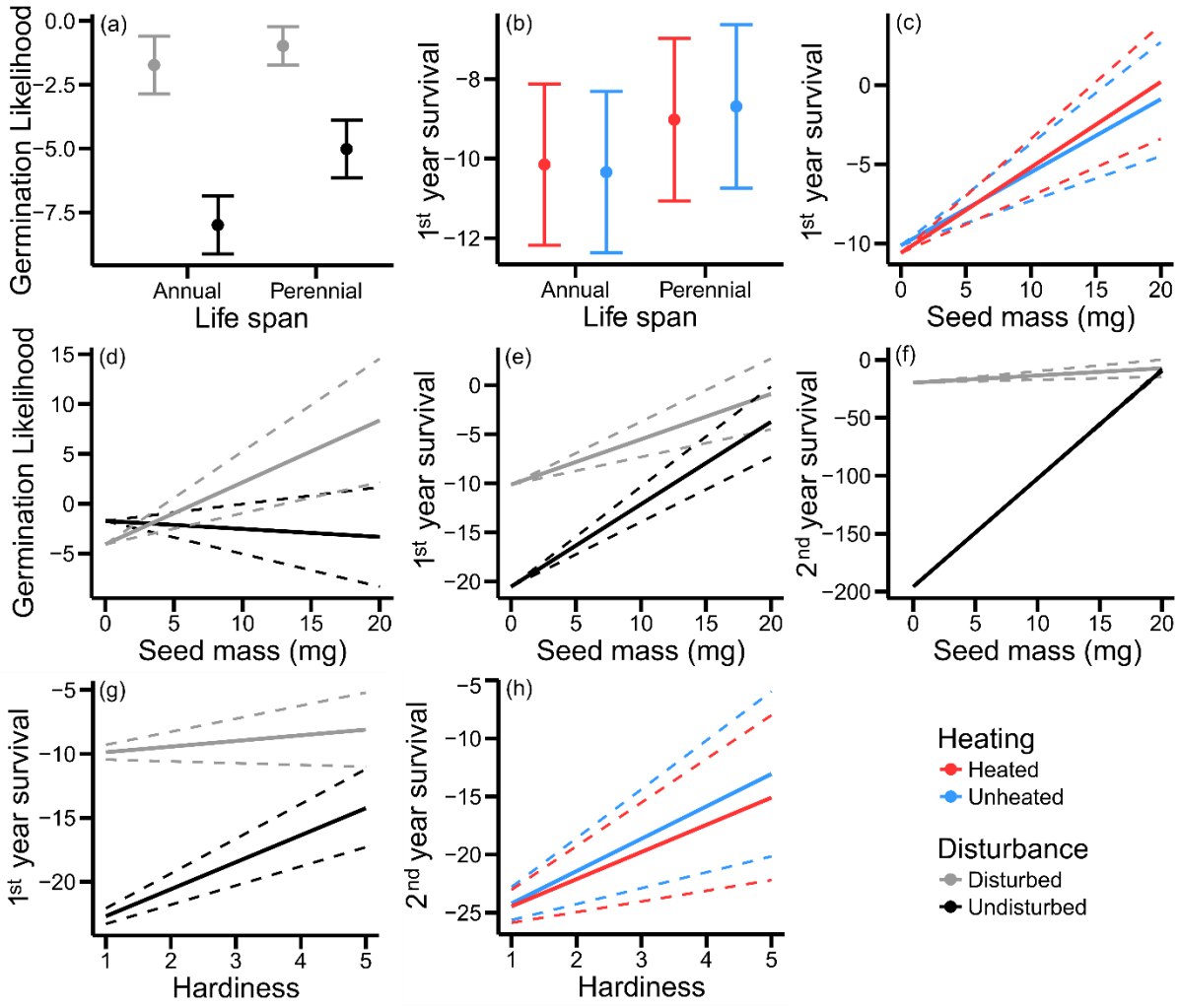

Fig. 3. (a) Effects (in terms of log odds and their standard errors) of life span on germination likelihood in disturbed (grey) and undisturbed (black) plots, and (b) on first-year survival in heated (red) and unheated (blue) plots. (c) Effects of seed mass on first-year survival in heated and unheated plots, and (d) on germination likelihood, (e) first-year survival and (f) second-year survival in disturbed and undisturbed plots. (g) Effects of hardiness on first-year survival in disturbed and undisturbed plots, and (h) on second-year survival in heated and unheated plots.